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Avian species and family composition along elevational and disturbance gradients in Santa Fe National Park, Veraguas Province, Panamá

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SIT Study Abroad

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Abstract

Elevational gradients are some of the most well-known and researched biological trends. However, how species diversity varies with elevation differs by taxa and location. One hypothesis suggests that bird diversity decreases with increasing elevation in the tropics. In addition, bird diversity may decrease along the forest edge and in areas of increasing disturbance. Therefore, in this study I surveyed avian diversity along an elevational gradient in Santa Fe National Park, Veraguas, Panamá using point-count observations. Thirty-six point-count locations in 3 elevation zones were surveyed between 19 Apr and 29 Apr 2017. Shannon diversity, richness, and evenness were calculated for both species and family, and were compared to elevation and disturbance level (a proxy for the forest edge). Although species diversity did not vary significantly with elevation or disturbance level, family diversity was significantly higher in high elevation regions and areas with a low level of disturbance. Measuring avian diversity along a larger elevational gradient stratified by disturbance level would further investigate the factors influencing bird diversity in Santa Fe National Park.

Acknowledgements:

This project would not have been possible without the tremendous support of many people. Special thanks go to Dr. Chelina Batista for helping refine my project objectives and methods, Josué Ortega and Michelle for allowing me to stay at their house throughout the duration of this study, for helping me work through the many logistical problems that arose, and for introducing me to the Santa Fe area, Jacobo Ortega for teaching me about the abundant bird life of the area and how to properly conduct point-counts, as well as arranging my accommodations for the first two nights, all of my SIT classmates for their sound advice, companionship, and moral support throughout this project, my parents (especially my mother, Dr. Lisa Shipley) for providing me with invaluable advice on research design, statistics, and writing, and finally Dr. Aly Dagang for encouraging all of us to reach our potential, and for providing an opportunity to pursue topics we are passionate about.

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Introduction

As the human population on Earth surpasses 7 billion, anthropogenic effects on the environment are becoming ever more pronounced. The consumption of natural resources by humans has instigated rapid worldwide climate change, habitat fragmentation, and invasion by non-native species. These changes have prompted a significant decrease in biodiversity, increase in extinction rates, and dramatic shifts in community assemblages and species ranges (Boyer and Jetz, 2014). Therefore, studying the natural biodiversity rate and the climatic tolerance of species is now more important and urgent than ever. These natural processes are often much more poorly understood than the artificial trends, but are no less critical to evaluating the increasing anthropogenic effects on our environment (Cadena et al., 2011).

Aside from the effects of human activities, species diversity and community composition varies widely on both latitudinal and elevational gradients. In 1967, Daniel Janzen linked those two gradients by introducing the "mountains are higher in the tropics" hypothesis. He stated that because climatic factors including temperature and precipitation vary much less in the tropics than in the higher latitudes, and because elevational changes cause changes in these climatic factors, mountains and high elevations provide more effective barriers to dispersal in tropical regions than they do in temperate and polar regions (Janzen, 1967).

The limited dispersal ability of tropical terrestrial vertebrates has been well documented in many taxa, including lowland forest birds (Moore, 2008), mammals (Munguia et al., 2008), and amphibians (McCain et al. 2009). This research provides support for Janzen's hypothesis, and suggests that mountain ranges may be relatively impermeable barriers to terrestrial dispersal for those taxa. However, the ubiquity of Janzen's hypothesis for birds has been called into question, and efficacy of these barriers of vertebrates is still under considerable debate (Brumfield, 2012; Smith et al., 2014). Although the research of Moore et al. (2008) suggests that lowland tropical birds cannot disperse well outside of the forest matrix, Smith and Klicka (2010) found negligible effects of elevation on the dispersal of tropical Mesoamerican birds. Likewise, Cadena et al. (2011) found that biotic factors such as competition and niche partitioning had a greater effect on the species ranges of tropical ectotherms and their ability to fill their fundamental niche than abiotic factors such as elevation and rainfall.

Another aspect of Janzen's hypothesis is its relevance to speciation. Because mountains theoretically provide barriers to dispersal, they also inhibit gene flow and therefore provide the potential for allopatric speciation. However, the exact mechanism of tropical speciation by thermal ranges is still under debate (Lawson, 2010). Niche conservatism (where new species retain ancestral elevational tolerances) has been suggested as the principal driver of avian diversity in subtropical birds in China (Qu et al. 2014), but niche divergence (the branching of ancestral niche traits) seems to be a better indicator of speciation patterns of parrotbill (Paraxadornis sp.) in the Himalayas to the south and west (Liu et al., 2016).

These contradictory results show that much more research is necessary to fully examine the relationships between tropical dispersal ability, elevation, and vicariant speciation. Specifically, the interaction between abiotic and biotic factors in shaping the ranges of tropical terrestrial species, and the ability of mountain ranges to block gene flow and support allopatric speciation must be examined more thoroughly for a clearer understanding of these relationships.

Because of the ecological importance and vulnerability of species living on mountain slopes (Guralnik 2007), preserving elevational gradients has become more critical to the success of biological diversity conservation. McCain (2010) predicted that bird diversity gradients in wet climates would follow a general "low-plateau" pattern, where low-elevation regions have a higher average species diversity on local scales. However, much of the protected areas in Central America are surrounding areas of higher elevation (see Cerro Hoya, Parque Internacional La Amistad, and El Cope National Parks as examples of high-elevation protected areas). This may indicate a disconnect between the current conservation system and the objectives of biodiversity conservation, if these protected areas are not actually protecting the greatest bird biodiversity.

Although protecting large expanses of untouched rainforest in a variety of elevation is the most visible and commonly used method of tropical conservation, protecting edge environments or ecotones (the boundaries between natural habitat types) is also crucial for biodiversity conservation (Ries and Sisk 2004). In fact, several studies have documented increased tropical passerine nest density at forest edges, despite a corresponding increase in nest predation (Battin 2004). This is due to the "ecological trap effect", where organisms will selectively choose poorer-quality habitats, despite no clear reproductive or fitness advantages (Battin 2004). Furthermore, some species may even be "edge specialists", living primarily along the forest edge (Ries and Sisk 2004). However, artificial disturbances and development can cause habitat fragmentation, leading to a decline in species abundance and diversity (Guralnik 2016, Battin 2004, Blair 1996). The effect of edge ecosystems on diversity is currently being overlooked within our current conservation system, and as a result, it is important to consider the effects of disturbance and forest edge on biotic communities.

This study attempted to combine Janzen's hypothesis and the current literature on diversity-elevational gradients with the hypothesized "ecological trap effect" and disturbance biology to describe the elevational-species diversity gradient in tropical understory birds and the response of avian communities to the incomplete conservation afforded them by Santa Fe National Park. My research objectives were to 1) Examine how the diversity, abundance, and evenness of birds changes along an elevational gradient in Santa Fe National Park and to 2) Determine the effects of Santa Fe National Park's infrastructure and anthropogenic disturbances on those bird communities.

Hypotheses:

- $H1_A$: Supporting the results of McCain (2010), increasing elevation corresponds to a decrease in species and family richness and diversity.
- $H1_0$: No relationship will be observed between elevation and avian diversity.

- $H2_A$: Because of increasing edge effects in areas of high disturbance, bird community composition will be different and diversity will be lower in areas of high disturbance than in areas of low disturbance.
- $H2_0$: No differences in bird diversity and community composition will be observed in locations with different levels of disturbance.

Methods

General Location and Collection Site

Santa Fe National Park is located at 8.5°N and 81°W, in the Veraguas Province in Central Panamá [Appendix I]. The National Park was created in 2001 by executive order, and protects 72,636 ha of tropical forest in the upper watershed of the Santa Maria River, the vast majority of which is practically inaccessible except by off-trail hiking. The National Park protects evergreen tropical lowland and montane forests, ranging from 300 to 1300 m. Because it contains the extreme eastern edge of the Central Cordillera in Western Panama, Santa Fe National Park protects a unique community assemblage of tropical lowland and highland species. More than 300 species of birds have been observed and identified in the National Park, making it one of the most biodiverse avian sites in the world.

To examine the effects of elevation on avian diversity, I chose three locations of different elevations to construct point-count transects. The "Low" elevation site stretched along Ruta 33 from the ANAM (Ministerio de Ambiente de Panamá) station to the west and ranged from 700-800 m, the "Middle" elevation site did the same to the west and ranged from 800-900 m and the "High" elevation site stretched along the "Sendero de Mariposas", a trail leading south from Ruta 33 up the side of Cerro Mariposa and ranged from 950-1150 m [Appendix I]. Although the middle and low elevation sites were very close together, there were no other alternatives for the placement of the low elevation transect within the National Park (see Discussion for possible biases and problems associated with the placement of these three locations)[Appendix I].

After completing a form for our Local Review Board (LRB) ensuring that no human participants would be at risk during this study, I began data collection on 19 Apr 2017.

Data Collection

Point-Counts

Over the span of 10 days, from 19 Apr to 29 Apr 2017, I conducted 120 10-minute point-counts (for a total observation time of 20 hours). Birds were counted at each transect location 3 times on 3 separate days, and the "High" elevation location was replicated 4 times, so that comparisons could be made between the "High" location and an aggregate of the two lower locations. All of the point-counts were conducted in the morning within 4 hours of local sunrise, or between 0630 and 1100 hours. To minimize temporal bias, the starting point of the point-count session alternated each session, and each location was sampled on alternating days. For 10 minutes at each point, I stood and recorded the number and species of each bird seen or heard. To save time, a 4-letter "code" was created that referenced the common names of each species [see Appendix II for a list of the bird codes]. Similar point-count methods may be found in Hanni et al. (2013) and Ávalos and Bermúdez (2016). The method of observation (whether by sight or sound) was also recorded. If possible, a photograph was taken of the bird for later identification. I identified each bird observed either in the field or by using the field guide *The Birds of Panama* (Angehr and Dean 2010).

Site Characteristics

Along with the bird observation data, I recorded general site characteristics. UTM Coordinates and elevation data were taken at each point along each transect using a GPS unit (Garmin GPSMAP 64s). To minimize errors associated with GPS inaccuracy, the elevation of each point was recorded each day and averaged. Next, the forest was classified based on its level of disturbance: Forests classified as showing high disturbance had a visible long-term human influence (e.g., a residence or ranger station), those showing medium disturbance had evidence of human influence one time or in the past (e.g. a clearing created during the road's construction), and those showing minimal influence were forested up to the edge of the road [Figure 1].

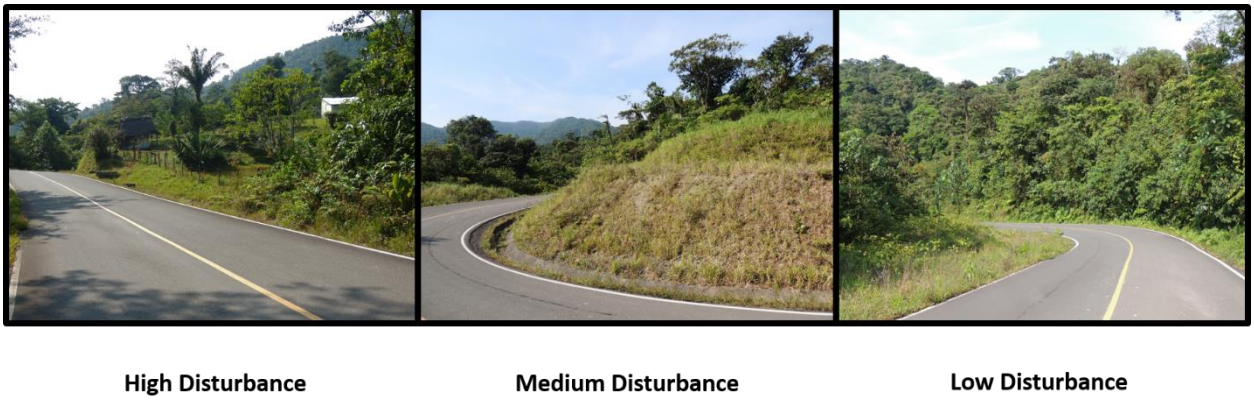


Figure 1: Photo examples of the three different disturbance categories, taken on 28 Apr 2017. The high disturbance picture (right) was taken at point M10, the medium disturbance picture (middle) was taken at L8, and the low disturbance picture was taken 40 m above L10.

Analysis:

All statistical analyses of the data collected were conducted on R (version 3.3.1) and RStudio (R Core Team). Packages used include the *plyr* package for rearranging data frames (Wickham 2011) and the *vegan* package for community ecology analysis (Oksanen et al. 2016). All of the graphs were likewise created in R unless otherwise noted.

Taxonomic Analysis

After completing each day's observation session and entering all of the observation data, I recorded the family name of each species observation, using *The Birds of Panama* (Angehr and Dean 2010), so that family-level analyses could be conducted. If the family name of a bird species was uncertain (*insertae sedis*), it was included as its own family (see Appendix II for a list of all bird species observed and their placement within the currently defined Neotropical bird families). I was unable to identify one species (UNK2, or Unknown 2) to the species level, but it was a member of the Emberizidae family and was placed as such. If a species was only observed by sound and I was unable to identify it even to the family level, it was not included in this study. Furthermore, Apodidae (swifts) and Accipitridae (hawks, eagles, and kites) were removed from the analysis because of the decreasing influence of small-scale elevation and disturbance changes on primarily aerial birds.

The most common families and species by abundance (number of observations) per location and disturbance were then calculated using a constructed function on R (see Appendix IV for a commented copy of the function).

Diversity Calculations

Using the *vegan* R package, the Shannon diversity index of each survey site ("low", "medium", or "high" elevation) and from Santa Fe National Park as a whole was calculated from the total species counts collected between 19 and 28 Apr. I chose Shannon diversity because of its ubiquity in community ecology (see Blair 1996, Gomez et al. 2006), its ease of calculation on R, and its relationship to species evenness indices. Likewise, the total family diversity was calculated at each location and for the National Park overall. Species richness and total abundance (number of individuals) was also calculated.

Based on the per-point and time observation results (n=120), the expected minimum species richness of the entire study site was calculated using several different methods of estimating species richness, including Chao, jackknifing, and bootstrapping. For a detailed explanation of these species richness estimators, refer to Gotelli and Colwell's chapter in *Biological Diversity* (2010). Also, I created a species-accumulation curve plotting the expected increase in species richness with an increase in sample size. The richness estimators and species-accumulation curve helped to ensure that an adequate sample size of point-counts was obtained during the course of the study. The species accumulations and richness estimations may be found in the Results, and a discussion of the implications of those graphs is located in the Discussion section of this paper.

Location and Disturbance Comparisons

Because each point location was only replicated three times (with the exception of those in the high elevation site), any statistical methods comparing the average of all 12 points in the entire location might not accurately reflect trends in the data and statistical power may be limited. Therefore, instead of comparing the average diversity over the entire transect, the average *per-point* diversity was calculated and compared over the three sites. After visually assessing that the data distributions were roughly normal, I conducted 2 one-way ANOVAs comparing species and family diversity across the different locations. Similarly, 2 one-way ANOVAs were conducted comparing species and family diversity trends among levels of disturbance. The final round of the "high" elevation survey was removed for this analysis, so that each location could have the same number of replicates.

Linear Models and ANCOVAs

After conducting the one-way ANOVAs comparing diversity values among disturbance levels and site location, I examined the relationship between elevation (an independent, continuous variable), and the species and family diversity values at each point using a linear regression. The regression's assumptions (normality of data, homoscedasticity, homogenous variances) were checked to ensure the proper use of a linear model. As before, the final round of the "high" elevation survey was removed to ensure a consistent number of temporal replicates.

Using linear regressions and ANCOVA tests, I also examined the other potential relationships between avian diversity and the explanatory variables I gathered:

1. Y ~ Elevation(x_1)
2. Y ~ Elevation(x_1)*Disturbance Level(x_2)
3. Y ~ Elevation(x_1)*Location(x_2)
4. Y ~ Disturbance(x_1)
5. Y ~ Disturbance(x_1)*Location(x_2)
6. Y ~ Location(x_1)
7. Y ~ Elevation(x_1)*Disturbance Level(x_2)*Location(x_3)

To compare between the models and to ensure the best model for the data, Akaike Information Criterion (AIC) values were calculated for each potential model.

Because the points in the "High" location were spread over a larger elevational range, a separate elevation model was created for just those points.

Results

For the 120 10-minute point-counts conducted, I observed a total of 652 individual birds from 79 species (R_S) and 27 families (R_F) [Appendix II]. The overall Shannon diversity index for species (H_S) of the observations was 3.819, whereas the Shannon diversity index for families (H_F) was 2.772. The evenness of the species (E_S) composition was 0.871 and family (E_F) composition was 0.841 [Table 1]. The minimum species richness estimations ranged from 89.54 (Chao estimator) to 98.86 (Jackknife) [Figure 2, App. II], and the species accumulation curve by each point-count was just beginning to asymptote [Figure 3, App. II].

The location with the highest species and family diversity, overall abundance, and richness was the "Middle" location, whereas the location with the most species and family evenness was the "High" location [Table 1]. Highest R_S, R_F, H_S, and H_F values were observed in the points with the lowest disturbance level [Table 1].

Table 1: Overall avian community characteristics for high, middle, and low elevation and disturbance levels.

Model Type	Community Characteristic	High	Middle	Low
Elevation	Species Richness (R_S)	45	**55**	50
	Family Richness (R_F)	18	**23**	20
	Shannon Species Diversity (H_S)	3.434	**3.569**	3.451
	Shannon Family Diversity (H_F)	2.618	**2.682**	2.443
	Community Evenness (Species) (E_S)	**0.902**	0.891	0.882
	Community Evenness (Family) (E_F)	**0.906**	0.855	0.816
	Abundance	172	**234**	199
Disturbance	Species Richness (R_S)	38	51	**61**
	Family Richness (R_F)	18	22	**23**
	Shannon Species Diversity (H_S)	3.338	3.416	**3.650**
	Shannon Family Diversity (H_F)	2.381	2.559	**2.754**

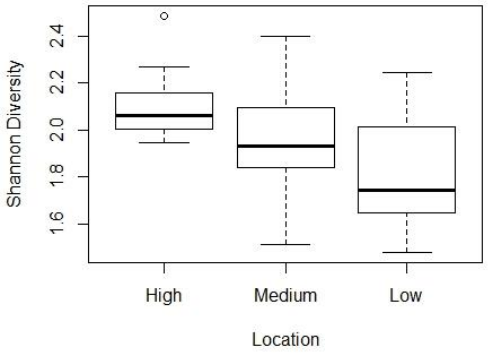
The most common species and families varied slightly among the locations [Table 2]. Thraupidae (tanagers) were the most commonly observed birds in the "Low" and "Middle" locations, whereas Columbidae (pigeons and doves) were the most commonly observed birds in the "High" location.

Table 2: The 10 most common bird families (highest abundance) observed in each of the site locations from 19 Apr to 29 Apr 2017. Bird species with uncertain taxonomic placement (Bananaquit and Saltador) are placed in their own families.

Rank	High	Middle	Low
1	Columbidae	Thraupidae	Thraupidae
2	Trochilidae	Troglodytidae	Emberizidae
3	Troglodytidae	Bananaquit	Tyrannidae
4	Bananaquit	Columbidae	Troglodytidae
5	Pipridae	Emberizidae	Bananaquit
6	Thraupidae	Tyrannidae	Columbidae
7	Thamnophilidae	Trochilidae	Turdidae
8	Ramphastidae	Icteridae	Trochilidae
9	Trogonidae	Ramphastidae	Parulidae
10	Tyrannidae	Pipridae	Hirundinidae

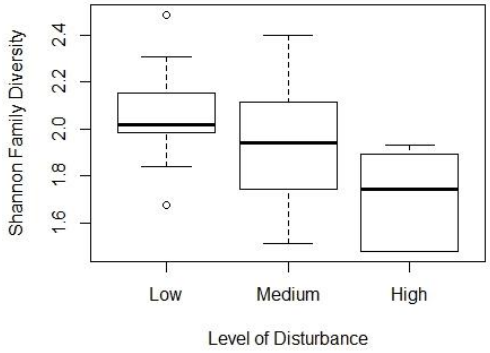
The mean family diversity per point varied across locations ($F=6.05$, $p=0.006$) [Figure 3], and across disturbance levels ($F=5.98$, $p=0.006$) [Figure 4], with the highest diversities recorded at the highest elevations and the lowest disturbance levels as predicted by my hypotheses. A Tukey's HSD test revealed a significant difference between the family diversity at the "Low" and "High" locations ($p=.004$), but not among any other combinations ($p=.276$ and $.151$). However, species diversity and evenness did not significantly vary across either location ($F=2.95$, $p=0.07$) or across disturbance level ($F=1.06$, $p=0.357$).

Figure 3: Mean bird family diversity compared across the three site locations ("High", "Middle", and "Low" elevations)



Overall, the species and family diversity at each point did not significantly vary with elevation (H_S: $p=0.898$, adjusted $R^2 = -0.029$; H_F: $p=.115$, adjusted $R^2 = .044$) [Figure 5]. Likewise, elevation alone did not influence species and family richness (R_s: $p=0.527$, adjusted $R^2 = -0.017$; R_F: $p=0.515$, adjusted $R^2 = -0.017$).

Figure 4: Mean bird family diversity compared across three levels of anthropogenic disturbance.



Of the 7 models for predicting bird diversity, the disturbance only model had the lowest AIC values for family diversity. The elevation only model was able to predict species diversity the best [Table 3 shows the full AIC values and weights]. However, the relationship between elevation and species diversity was still insignificant (p=0.898).

Table 3: AIC values and weights for H_F and H_S.

Models	H_F		H_S	
	AIC	Weight	AIC	Weight
Elevation	2.149996	0.097041	**-2.85739**	**0.320343**
Elev*Dist	2.398352	0.085709	3.984929	0.010467
Elev*Loc	0.674693	0.202915	-2.12274	0.221864
Location	**-0.49464**	**0.364109**	-1.35637	0.151242
Disturbance	3.293644	0.029241	1.930237	0.054779
Loc*Dist	0.917072	0.179755	-2.24334	0.235655
Elev*Dist*Loc	5.793877	0.015693	1.80139	0.031187

For all 4 survey rounds for the "High" location, elevation was a generally poor predictor of family diversity (p=0.200, adjusted R^2 = .074), but was better (if still non-significant) at predicting species diversity (p=0.084, adjusted R^2 = 0.196) and species richness (p=0.070, adjusted R^2 = 0.221) [Figure 6].

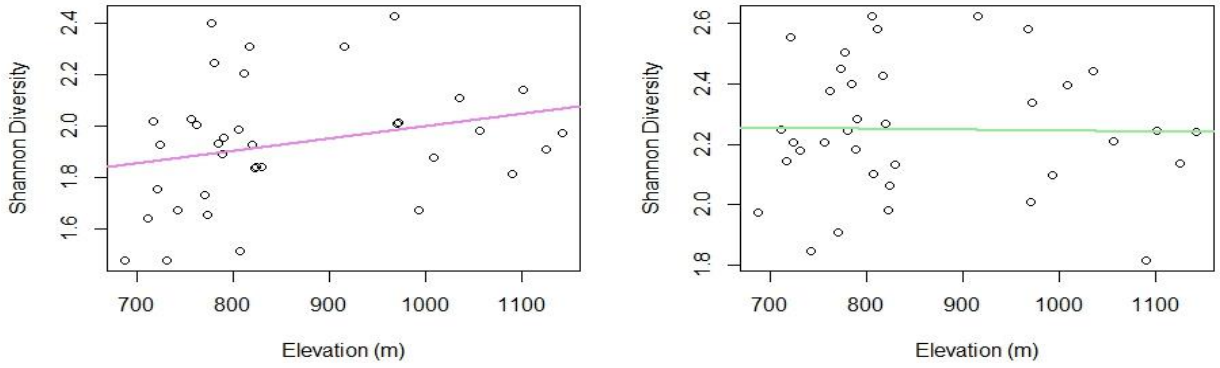


Figure 5: Regressions plotting the relationship between elevation and H_S (left), and H_F (right) for all site locations. Neither relationship is statistically significant. In Santa Fe National Park, Panamá.

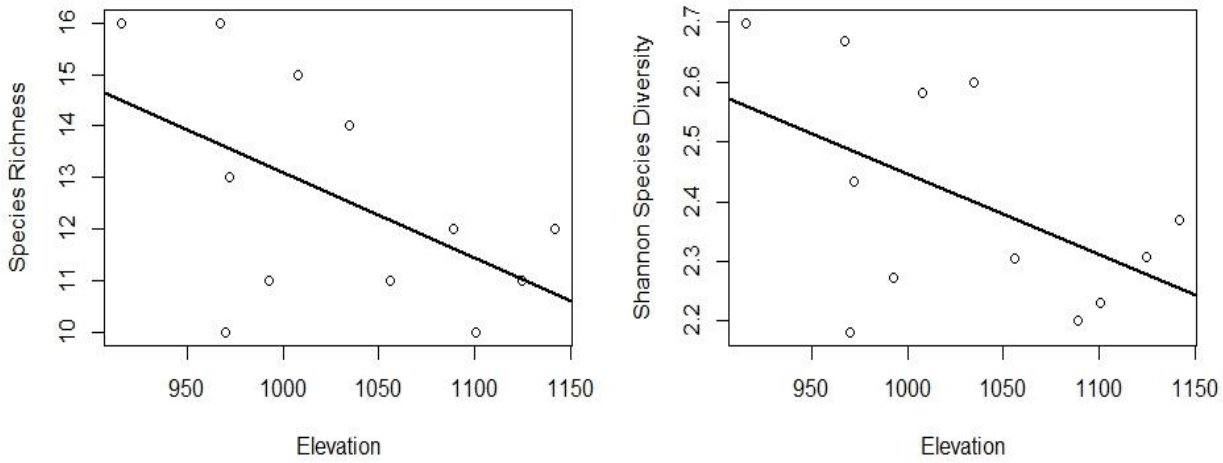


Figure 6: Regressions plotting the relationship between elevation and R_S (left) and H_S (right). Although neither relationship is statistically significant, a clear downward trend is exhibited in both graphs, and, with more sampling, the relationship might achieve statistical significance.

Discussion

Through this study, I compared tropical avian community characteristics using point-count surveys (Shannon family and species diversity, family and species evenness, species richness) to site characteristics such as elevation and anthropogenic disturbance level. I was able to quantify changes in avian communities across differing landscapes and elevations during the beginning of the wet season in Santa Fe National Park.

Overall Community Characteristics

The three species-richness estimators used, extrapolating from the observations at each sampling event (each ten-minute point-count session), give minimum species richness values ranging from 90 to 100 total species [App. III, Figure 1]. These estimations are relatively close to the actual species richness observed (79), but they indicate that conducting a few more point-counts may have been necessary to obtain a more accurate estimate of the true species richness and diversity of the locations. As a whole, Santa Fe National Park is home to roughly 300 bird species, and therefore it is clear that the data collected cannot be extrapolated or generalized to a larger area (such as the entire National Park). However, the species accumulation curve [App. III, Figure 2] began to reach an asymptote, which suggests that the amount of point-count surveys conducted were at least close to the amount needed to represent the observed avian communities adequately, at least on a small-scale.

The overall rank-abundance curves [Figure 7] for the study indicate an avian community dominated by rare species (60 species were observed fewer than 10 times). This rare-species dominant community is similar to the community observed by Ávalos and Bermúdez (2016) in a premontane rainforest in Costa Rica. The family rank-abundance curve suggests a more even distribution of bird family than species, with 9 families observed more than 40 times. However, 2

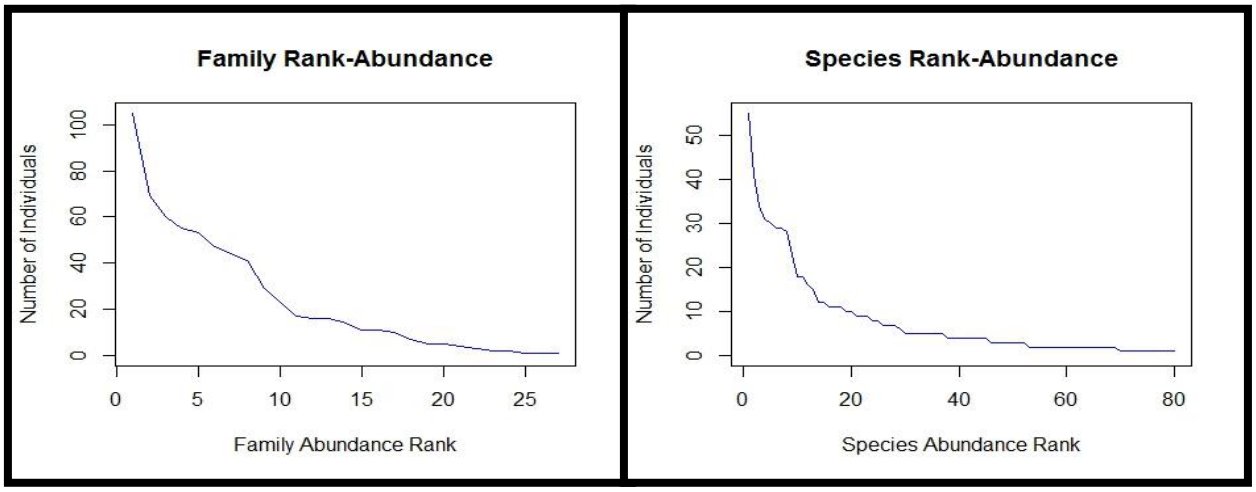


Figure 7: These rank-abundance graphs plot the total abundance of observed birds in number of observations per family (left) and species (right).

of the families recorded (Bananquit and Saltador) are only monotypic with uncertain taxonomic placement, and therefore may influence the rank-abundance of the bird families observed, as well as the family diversity and other family characteristics. This is especially true for the Bananaquit, which, due to its distinctive call, was identified 55 times (40 by sound).

The three most common families observed throughout the study were Thraupidae (tanagers), Troglodytidae (wrens), and Emberizidae (finches and relatives). Many of the commonly-observed species in these families are found in edge zones and ecotones (Angehr and Dean 2010), and therefore the abundant presence of these species indicate a habitat that is in close proximity to areas without dense canopy cover and/or disturbed areas. Because the sampling for the lower two locations was done along a two-lane paved road, the abundance of these "edge-adapted" birds is not unexpected.

Diversity Characteristics by Location and Elevation

Following from McCain (2010) and other elevational-species diversity studies (Munguia et al. 2008, Qu et al. 2014, Liu et al. 2016), I expected the highest diversity of birds to be found at the lower and middle elevation sites, preceding a decline in diversity in the upper elevations. This hypothesis was only partially supported by the data. The overall species richness, family richness, and species diversity values for each location [Table 1] follow the predictions, with the lowest values observed at the "High" elevations. However, overall family diversity was the lowest at the "Low" elevation.

These results suggest that, in fact, lower elevations have a higher species diversity and richness than high elevations. This may be because of the generally warmer climate in the foothills of Santa Fe National Park than on the mountain slopes. Janzen's hypothesis states that, because of the low seasonality and moderate climate in areas with low latitude, mountain ranges are less hospitable than in temperate and polar regions (Janzen 1967). As a result, a decrease in species diversity should be predicted with increasing elevation, a trend observed by McCain (2010).

When comparing individual points, H_S did not vary significantly with the location. However, H_F was significantly higher per-point in the "High" location than in the "Low" location [Figure 3]. This discrepancy between the H_S and H_F values may be due to cryptic species diversity (different species that are morphologically similar or identical to one another), or because many species of some families (e.g. Thraupidae, 14 species observed) were observed, whereas very few species of some families (e.g. Troglodytidae, 4 species observed) were observed.

The most common families of each survey location reflected the significant difference in family diversity across the locations. The most common families observed in the "medium" and "low" locations were Thraupidae, Emberizidae, and Troglodytidae. Many of the birds observed within these families are commonly referred to as "habitat generalists", able to survive with a wide range of environmental and disturbance factors, which may explain their presence in the comparably more-disturbed "low" and "middle" elevations (Angehr and Dean 2010). However, of those families, only Troglodytidae was among the 5 most common families observed in the "high" survey location. Trochilidae (hummingbirds) and Pipridae (manakins) were also observed in much higher relative abundances in the "high" location than in the "middle" or "low" locations. This may indicate that Trochilidae and Pipridae prefer higher elevations and more heavily forested areas, which *The Birds of Panama* (Angehr and Dean 2010) suggests.

Despite the differences in family abundance and H_F among location, linear regressions between the elevation of each point and R_F, R_S, H_F and H_S failed to reject the null hypothesis. This is in direct contrast to the research performed by Kluge et al. (2006) that suggested a clear hump-shaped relationship between pterodyte (fern) species diversity and elevation in Costa Rica, as well as McCain (2010), which found support for a low-diversity plateau in tropical Mesoamerican regions. There are several factors that may have influenced these results. First, the entire range of elevations sampled stretched from 720 to 1150 m, and were entirely located on the southern border of the park. This range may not have been large enough to properly examine the elevational gradient of Santa Fe National Park. For example, Kluge et al. (2006) sampled from site ranging from 40 to 2400 m, more than 5 times the elevational breadth of this study.

These results have many conservation implications. The results suggest that areas of lower and middle elevations have higher family richness than high elevations. Many tropical protected areas are centered on highland regions, where endemism and specialization are high (Munguia 2007, Cadena et al. 2011). For example, Parque International La Amistad, a UNESCO World Heritage Site and widely considered a paradigm in biodiversity conservation, begins at a certain elevation, only protecting the areas above the boundary. However, the results of this study may imply that, to protect the greatest number and diversity of families, these parks should also

attempt to protect lowland areas and non-forest landscapes (for example, tropical savanna and humid grasslands).

A potential covariate that affected the results was the differing habitat types across the locations. Although the "low" and "middle" point-counts were conducted along a two-lane paved road surrounded by a mixture of dense forest, low-lying shrubs and bushes, and small (<50 m^2) areas of grass-dominated vegetation, the point-counts conducted in the "high" location were along a trail directly through the dense forest. These differences in habitat across location sites may have influenced the species composition at each site. Because of this, I categorized the habitats at each point count into disturbance zones in order to account for changes in habitat across point-counts.

Diversity Characteristics by Disturbance:

I hypothesized that a general decrease in diversity would be observed with increasing anthropogenic disturbance. Therefore, I predicted that highly disturbed areas would have less diversity than undisturbed areas ($H2_A$). The results supported this hypothesis, with the highest diversity and evenness values found in areas of low disturbance [Table 1], average family diversity per-plot observed in areas of low level of disturbance, and the lowest diversity observed in point with a high level of disturbance. However, the variance in family diversity was much higher in plots with a moderate level of disturbance than in areas with a high or low level of disturbance [Figure 4].

Many studies have been conducted on "edge effects" such as those observed in the southernmost region of Santa Fe National Park (Leopold 1933, Battin 2004, Barlow et al. 2007). However, the actual response of animals to forest edges and habitat disturbance and fragmentation is still under debate. Barlow et al. (2007) examined the species richness and diversity of 15 vertebrate and invertebrate taxa at a primary forest site, a secondary forest site, and a disturbed plantation site. They found that bird species richness and diversity was higher in the primary forests than in the disturbed areas, reflecting the data collected in this study. However, for many of the other taxa (e.g. moths, bees), Barlow et al. (2007) found unclear relationships or even positive relationships between forest disturbance and diversity. A hypothesis that attempts to explain the inverse relationship between bird diversity and disturbance is the "nest predation" hypothesis, which predicts that nest predation is high near forest edges. However, in a synthesis of *a priori* literature conducted by Lahti (2001) found that the majority of studies on birds in edge habitats did not report an increase rate in nest predation. The mechanism of the "edge effects" in birds is still uncertain, and future studies are needed to further examine the cause of the effects observed in this study and many others.

In this study, bird family diversity varied across the levels of anthropogenic disturbance, but species diversity and evenness had no significant differences among the disturbance levels. This trend closely mirrors the differences observed in family and species diversity across location levels. This similarity, coupled with the collinearity of disturbance and location (the "high" location was entirely low disturbance, whereas the "low" location was primarily moderately or heavily disturbed, indicates that either disturbance or location is a masking variable for the other. Because the elevation-diversity regressions showed an insignificant linear relationship, it is

probable that location acts as a masking variable for the true effect of disturbance level on bird family diversity.

Furthermore, the disturbed areas of the study site had, in general, higher visibility than the forest areas without human disturbance. This may have introduced a systematic bias into the study, as the identification and observation of birds was primarily visual. In addition, birds acclimatized to disturbed areas may also be more habituated to the humans that occupy those areas, and therefore are able to be observed much more easily than forest species.

Conclusion and Areas for Future Study

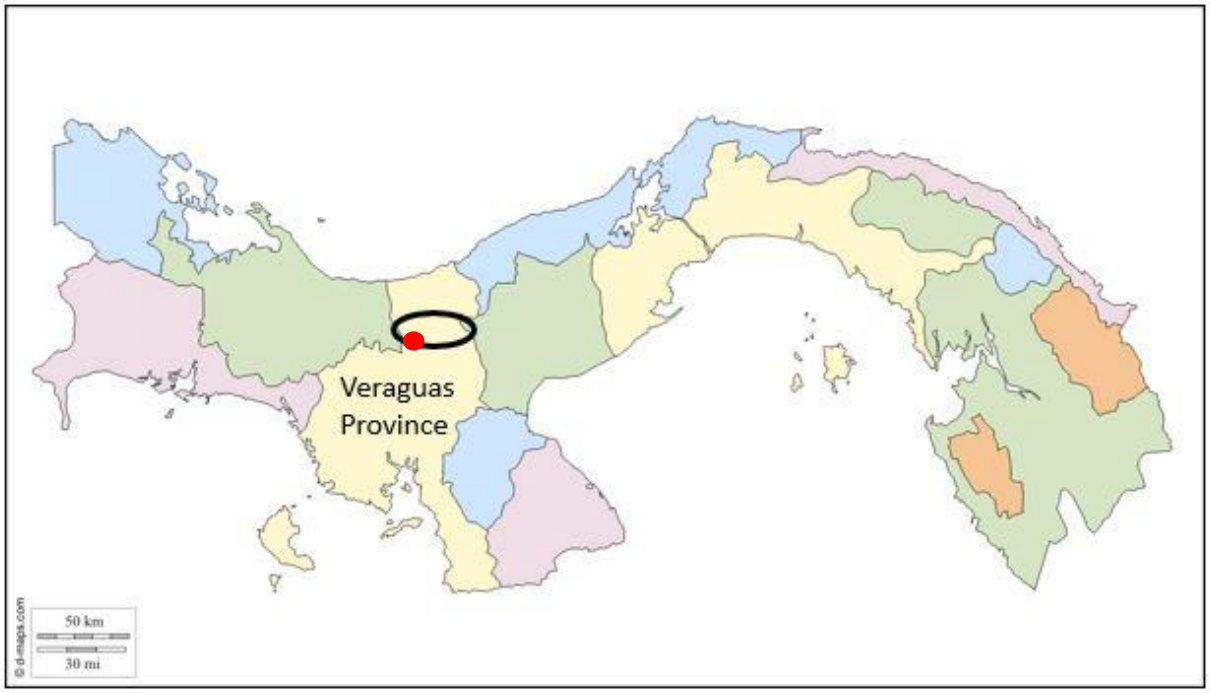
These results of this study showed an unclear and ambiguous relationship between elevation and avian community characteristics in Santa Fe National Park, but significant differences in diversity across different disturbance levels. However, the selected locations for the study, the limited study time, and the inexperience of the researcher in identifying birds and conducting point counts, may have influenced the results. Therefore, more research is necessary to properly examine the three-way relationship between elevation, disturbance, and avian community characteristics in Santa Fe National Park. A study specifically examining elevational gradients in a particular habitat (e.g.: along Ruta 33 from the town of Santa Fe to Altos de Piedra, or along the Sendero Mariposas to Cerro Tute) would remove the added covariate of habitat type and would more clearly define the species-elevation relationship for the habitat of that area. A study focusing on a specific functional group or taxon and their response to both elevation and disturbance would also fill an underserved niche. Edge species such as Thraupidae spp. and Tyrannidae spp. could be especially important species to study, because of their relative prevalence in areas of high and moderate disturbance. As habitat fragmentation continues to increase the amount of edge forest in tropical regions, understanding the response of these species and of birds in general to the forest edge is crucial to understand diversity patterns throughout the world.

This study also highlighted a difference between species and family diversity. Although species diversity was not influenced by elevation or disturbance, family diversity was. This indicates that family diversity may be more responsive to landscape and habitat changes than species diversity. A potential future study could examine these patterns in multiple places throughout Panamá to determine whether family diversity is actually a more sensitive metric of environmental changes, despite species diversity having a more defined role within conservation biology.

Human influence on the environment is rapidly expanding and may soon become irreversible (Guralnik 2007). As a result, studying how those changes affect the natural distribution and community structure of organisms with limited dispersal ability (e.g. tropical understory birds) is crucial for determining “at-risk” habitats and influencing research and conservation policy. By comparing bird community responses to elevation and disturbance levels, my research examined these patterns in the context of conservation. Although many trends were inconclusive and cannot be extrapolated to other locations or habitats, the research showed that unchecked human expansion and fragmentation can dramatically influence the community composition and diversity of birds in Santa Fe National Park.

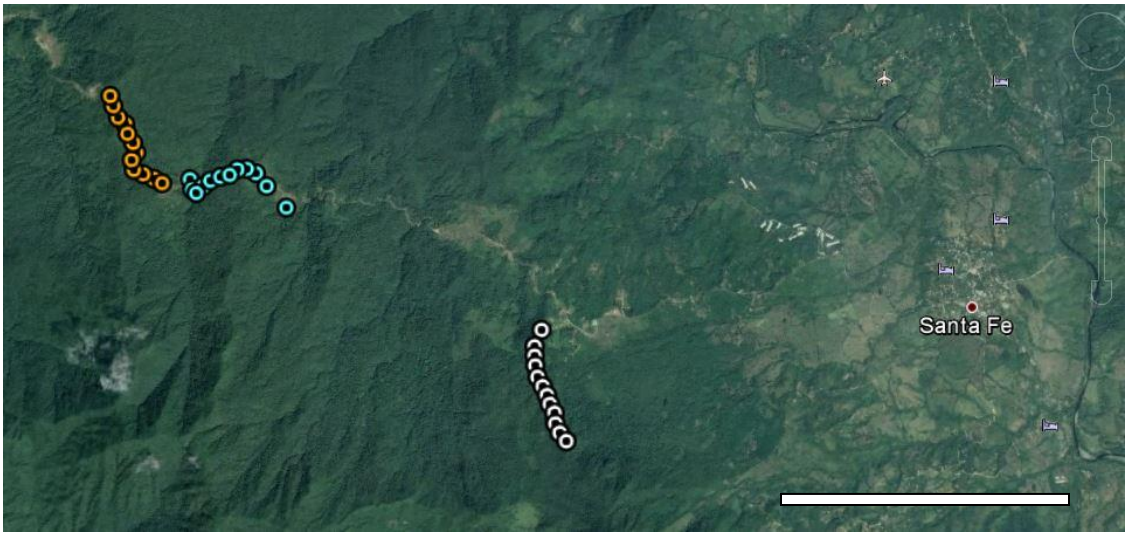
Appendix I: Relevant Study Maps

General Locator Map



A map of Panama and its provinces. Santa Fe National Park (the back oval) is located in northern Veraguas Province, and the the study site (red dot) was situated at the extreme southwestern edge of the park.

Site Location Map



A map of the points used in the pointcount transects. The white points are “High” elevation, orange are “Medium” elevation, and blue are “Low” elevation points. The town of Santa Fe is shown on the right for reference. The white bar scale bar in the lower right is roughly 3 km long

Appendix II: List of Bird Species Observed

Species Code	Common Name	Family Name	Location			Disturbance		
			H	M	L	H	M	L
BBGQ	Blue-black Grassquit	Emberizidae	•					•
BBWQ	Black-Breasted Wood-Quail	Odontophoridae	•					•
BGRT	Blue-gray Tanager	Thraupidae	•		•	•		•
BGTG	Blue-and-Gold Tanager	Thraupidae		•	•		•	•
BHPR	Brown-hooded Parrot	Psittacidae	•					•
BLGU	Black Guan	Cracidae	•					•
BNNQ	**Bananaquit**	***insertae sedis***	•	•	•	•	•	•
BRVE	Brown Violet-Ear	Trochilidae	•					•
BSSP	Black-Striped Sparrow	Emberizidae	•	•	•	•	•	•
BTFG	Buff-Throated Foliage Gleaner	Furnariidae		•			•	
BTGB	Black-Thighed Grosbeak	Cardinalidae		•			•	
BTSL	**Buff-Throated Saltador**	***insertae sedis***	•	•		•	•	•
BYTG	Black and Yellow Tanager	Thraupidae	•	•	•	•	•	•
BYWR	Bay Wren	Troglodytidae	•	•	•	•	•	•
CBTG	Common Bush-Tanager	Thraupidae	•	•			•	•
CCTG	Crimson-Collared Tanager	Thraupidae		•	•	•		
CCTH	Clay-colored Thrush	Turdidae	•	•	•	•	•	•
CHOR	Chestnut-headed Oropendola	Icteridae			•		•	
CSWB	Chestnut-sided Warbler	Parulidae		•	•	•		•
DFTG	Dusky-faced Tanager	Thraupidae	•	•	•		•	•
EWPW	Eastern Wood-Peewee	Tyrannidae	•		•		•	•
FRTG	Flame-rumped Tanager	Thraupidae	•	•	•	•	•	•
GBWP	Golden-brown Woodpecker	Picidae	•	•		•		•
GBWW	Gray-Breasted Wood-Wren	Troglodytidae	•	•	•	•	•	•
GHCH	Gray-headed Chachalaca	Cracidae	•					•
GHTG	Gray-headed Tanager	Thraupidae		•	•		•	•
GICB	Giant Cowbird	Icteridae		•	•	•		
GRHC	Green Honeycreeper	Thraupidae		•	•	•	•	
GRHR	Green Hermit	Trochilidae	•	•			•	•
GRKI	Great Kiskadee	Tyrannidae		•	•	•	•	•
GRTI	Great Tinamou	Tinamidae		•	•	•	•	
GTGK	Great-tailed Grackle	Icteridae		•		•	•	
HSWR	House Wren	Troglodytidae		•	•	•	•	
KBTC	Keel-billed Toucan	Ramphastidae	•	•	•	•	•	•
LBHR	Long-Billed Hermit	Trochilidae	•					•
LSEL	Lesser Elaenia	Tyrannidae	•	•	•	•	•	•
LTTR	Lattice-tailed Trogon	Trogonidae		•			•	•
MTEL	Mountain Eleana	Tyrannidae	•	•		•		•

MTTH	Mountain Thrush	Turdidae	•					•
OBTG	Orange-bellied Trogon	Trogonidae	•	•	•			•
PBQD	Purplish-backed Quail-Dove	Columbidae	•					•
PLAV	Plain Ant-Vireo	Thamnophilidae	•					•
RDQD	Ruddy Quail-Dove	Columbidae	•					•
RFMR	Rufous Mourner	Tyrannidae		•	•	•		•
RLHC	Red-Legged Honeycreeper	Thraupidae		•	•		•	
RTFC	Ruddy-Tailed Flycatcher	Tyrannidae	•					•
SBPI	Short-billed Pigeon	Columbidae	•	•	•	•	•	•
SCPI	Scaled Pigeon	Columbidae	•	•	•	•	•	•
SHHC	Shining Honeycreeper	Thraupidae			•	•		
SNCP	Snowcap	Trochilidae		•			•	
SPTG	Speckled Tanager	Thraupidae		•		•		
SRCC	Scarlet-rumped Cacique	Icteridae		•	•	•	•	•
SRWS	Southern Rough-winged Swallow	Hirundinidae			•	•	•	
STHM	Sapphire-Throated Hummingbird	Trochilidae			•		•	
STHR	Striped-Throated Hermit	Trochilidae	•	•	•		•	•
STKT	Swallow-tailed Kite	Accipitridae	•					•
STTG	Slaty-Tailed Trogon	Trogonidae	•		•			•
SWPK	Sulphur-Winged Parakeet	Psittacidae	•	•	•	•	•	•
TBEU	Thick-Billed Euphonia	Fringillidae			•	•	•	
TCEU	Tawny-Capped Euphonia	Fringillidae		•			•	
TCTG	Tawny-Crested Tanager	Thraupidae		•	•		•	•
TNWB	Tennessee Warbler	Parulidae	•	•	•	•		•
TRGN	Tropical Gnatcatcher	Sylviidae	•	•	•		•	•
TRKI	Tropical Kingbird	Tyrannidae		•	•		•	
UNK2	Unknown 2	Emberizidae		•	•	•	•	•
VBSD	Variable Seed-eater	Emberizidae	•	•	•	•	•	•
VCWN	Violet-Crowned Wood-Nymph	Trochilidae	•	•			•	•
VHHM	Violet-headed Hummingbird	Trochilidae	•	•			•	•
VLSB	Violet Sabrewing	Trochilidae	•					•
VLTG	Violaceous Trogon	Trogonidae	•					•
WBWW	White-breasted Wood Wren	Troglodytidae	•	•	•		•	•
WCSW	White-collared Swift	Apodidae	•	•	•		•	•
WLTG	White-lined Tanager	Thraupidae			•	•		
WNJB	White-Necked Jacobin	Trochilidae	•	•	•	•	•	•
WRMN	White-Ruffed Manakin	Pipridae	•	•	•	•	•	•
WSAS	Western-Slaty Antshrike	Thamnophilidae	•	•	•		•	•
WTDV	White-tipped Dove	Columbidae	•	•	•		•	•
WVEU	White-Vented Euphonia	Fringillidae		•	•	•	•	•
YCTR	Yelow-Crowned Tyrranulet	Tyrannidae	•	•	•	•	•	•

Appendix III: Species Accumulation and Estimation

Figure 1: **Species richness predictors**. Species-accumulation curves using three different species richness predictors (Bootstrap, Chao, and Jackknife) show the minimum expected species richness of the study site based on the per-point and time observations.

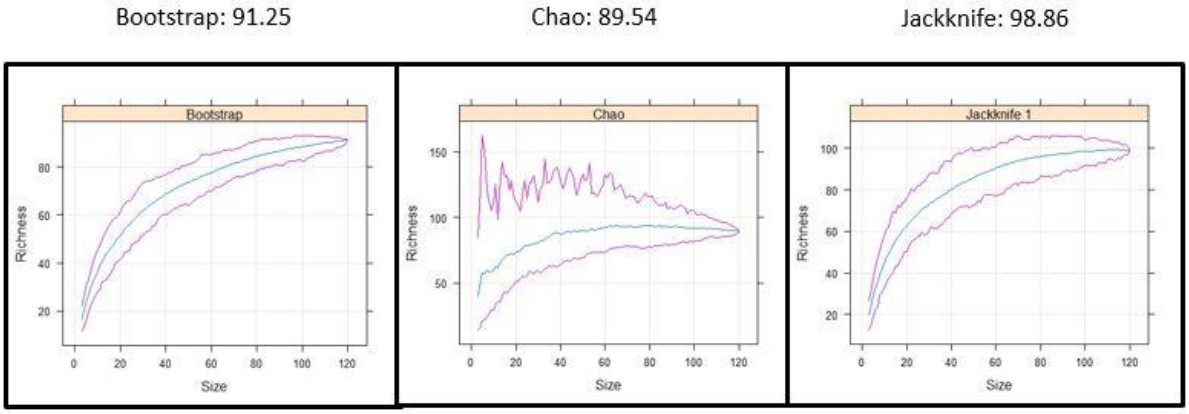
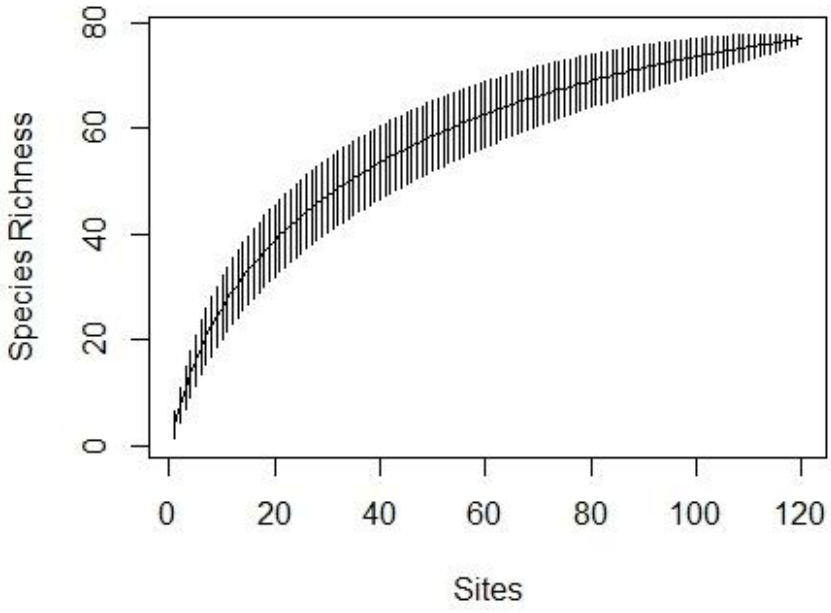


Figure 2: Species accumulation curve: This graph shows the predicted species richness found given a certain number of samples (individual point-count observations). As more samples are conducted, the total species richness of the study increases at a diminishing rate.



Appendix IV: Equations and Functions

Shannon Diversity (H):

$$H = -\sum_{i=1}^{R} p_i * \ln p_i$$

Evenness (E):

$$\frac{H}{\ln(R)}$$

Function 1: The most common taxa for each treatment

```
CommonTaxa=function(X,Y,Z){
  #X is the vector of the treatment
  #Y is the observation data vector
  #Z is a single number indicating the amount of taxa wanted
  CommonTaxaTable=table(X,Y)                          #This gives you species counts
  Levels=levels(X)                                    #The categorical levels
  CommonFrame=as.data.frame(CommonTaxaTable)          #This turns the table into a dataframe
  TaxaRank=c(1:Z)                                     #To get the correct number of Taxa
  NewFrame=data.frame(TaxaRank)                       #This is the frame we will be filling
  for(i in 1:length(Levels)){
    b=CommonFrame[CommonFrame[,1]==Levels[i],]        #Subsetting the data based on levels
    V=b[order(b$Freq,decreasing=TRUE),]               #ranking the species based on abundance
    VZ=as.vector(V[1:Z,2])                            #Making that a vector
    NewFrame[,i+1]=VZ                                 #entering it into the new dataframe
  }
  names(NewFrame)=c("TaxaRank",Levels)
  return(NewFrame)
}
```

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